VIII. *On the Development of the Teeth of the Newt, Frog, Slowworm, and Green Lizard.* *By* CHARLES S. TOMES, *M.A.* *Communicated by* JOHN TOMES, *F.R.S.*

Received July 23,—Read December 10, 1874.

THE researches of GOODSIR, constituting as they did a very material advance in knowledge, became so deeply graven upon the minds of scientific men that subsequent investigations, tending to modify his conclusions in important particulars, have attracted less attention than is their due.

As long ago as 1853 Professor HUXLEY (Quart. Journ. Microscop. Science, vol. i.) published the statement that, in the frog and mackerel at all events, the tooth-germs are at no time in the condition of free papillæ; and in the same paper correctly described the connexion existing between the oral epithelium and the enamel-organ in the fully formed dental sacs. Thus, although Professor HUXLEY accepted as in most particulars accurate the account given by GOODSIR of the sequence of events in the formation of the human tooth-sac, he in some degree anticipated the discovery made by Professor KÖLLIKER some years later (Zeitschrift f. wiss. Zool. 1863), that in several Mammalia the tooth-germs never pass through any papillary stage, but are from the first deep below the surface.

These observations have been confirmed and extended by WALDEYER (see his article in STRICKER'S 'Histology,' Syd. Soc. Translation, p. 481), by DURSY (Entwickelungsgeschichte des Kopfes, 1869), and by LEGROS and MAGITOT (Journal de l'Anat. et Phys. Ch. Robin, 1873); and it has been established to full demonstration that in mammals

i. There is never, at any stage, an open groove from the bottom of which papillæ rise up.

ii. That the first recognizable change in the vicinity of a forming tooth-germ is a dipping down of a process of the oral epithelium, looking, in section transverse to the jaw, like a deep simple tubular gland, which descends into the submucous tissue and ultimately forms the enamel-organ.

iii. That subsequently to the descent of the so-called enamel-germ, the changes in the subjacent tissue resulting in the formation of the dentine-papilla take place opposite to its end, and not at the surface.

iv. That the permanent tooth-germs first appear as offshoots from the epithelial process concerned in the formation of the deciduous tooth-germ (KÖLLIKER)—the first permanent molar being derived from a primary dipping down (like a deciduous tooth), the second deriving its enamel-germ from the epithelial neck of the first, and the third from that of the second (LEGROS and MAGITOT).

The error in GOODSIR's observations was not a very radical one, and was probably, at that date, almost inevitable, inasmuch as the processes by which more modern investigators have the advantage of seeing structures *in situ* were not then discovered: nevertheless, though the error in fact was not great, the deductions based upon it effect a wider divergence from the truth; and the terms "papillary stage," "follicular stage," &c. should be abandoned, as inapplicable to the phenomena observed in any teeth whatever which have been satisfactorily examined. The development of the simple teeth which have no enamel, and that of the teeth of Fish, Batrachia, and Reptilia, has been but little investigated, though the very early appearance of the enamel-germ in other Mammalia lends an additional interest to the inquiry.

I was myself fortunate enough to obtain specimens of fœtal armadillos, from which I was able to establish that, although not a particle of enamel was formed, the sequence of events was identical with that observed in other mammals*, viz. a dipping down of epithelium to form an enamel-organ, which differed in minor respects only from that found where enamel is really formed (Quart. Journ. Microsc. Science, Jan. 1874).

The literature relating to the development of the teeth in Batrachia and Reptiles is somewhat scanty.

Professor OWEN, in his 'Anatomy of Vertebrates' (vol. i. p. 389), reiterates the statement contained in his 'Odontography,' where he says, "The teeth of Reptiles are never completed at the first or papillary stage; the pulp sinks into a follicle and becomes enclosed by a capsule;" while a more detailed description is given of the process as it occurs in the frog, to be again referred to. He also states, "Dentine and cement are present in the teeth of all Reptiles."

He also draws comparisons between the condition permanently retained in reptiles and various transitory stages of human dentition, which are necessarily open to the same objections which apply to his descriptions of development, inasmuch as they arise out of these latter descriptions.

Some advances, however, towards a more correct appreciation of the process have been made. In the paper of Professor HUXLEY's already referred to, it is more than once clearly stated that the teeth of the frog do not pass through any papillary stage, but from the first are contained in sacs beneath the surface; and some years later Dr. LIONEL BEALE (Archives of Dentistry, 1864) published some observations upon the common newt, in which he found that the whole process of formation of the tooth-sac took place beneath the epithelium, which was intimately concerned in its formation. I am unable to entirely concur in his description of either the mode of origin or the structure of the tooth-sacs; but I have less hesitation in expressing a difference of opinion from

* My attention has since been drawn to an observation of Professor TURNER's, who found a structure homologous with the enamel-organ in a narwhal (Journal of Anat. & Phys. Nov. 1872); this, which I had overlooked, is, I believe, the first notice of a functionless enamel-organ; but unfortunately sections showing its structure and relations undisturbed do not appear to have been made, he having other and more important points under investigation in this same specimen.

so careful and skilled an observer, inasmuch as I am convinced that the facts can hardly be made out without studying hardened sections, a method of manipulation not, I believe, in this instance practised by him.

A few years subsequently LEYDIG (who appears to have overlooked Dr. BEALE's paper) published, in the 'Archiv f. Naturgeschichte' (1867), an account of the development of the teeth of the Salamander, in which he arrives at conclusions very similar. He believes that the tooth develops in a sac which is a purely epithelial formation, and that the tooth-papilla, and hence the whole tooth, is entirely epithelial. The figures which he gives are, however, far from being accurate representations of what takes place in the newt; but I have been so unfortunate as to fail in procuring a fresh salamander this summer. SANTI SIRENA (Centralblatt f. d. med. Wiss. No. 48, 1870) gives a brief account of an examination of some Batrachians and Reptiles; but there are no figures, and the descriptions are too short to be very definite. Grouping the Frogs and Lizards together, he states there are no marked differences to be noted from the process as known in Mammalia, save that the teeth become attached to the bone by the ossification of the tooth-sac; he contrasts the development of the frog's tooth, which takes place in a special sac, with that of the newt, which he states to be developed freely* in the mucous membrane.

The newt (*Triton cristatus*) being in some particulars easier to study than the other creatures examined, I will commence the description of my own observations upon it.

The teeth, examined without any prior treatment with acids, are seen to terminate in two unequal cusps†, sharply pointed, strongly refractive, and of a clear brownish yellow colour, which recalls that of many rodent incisors (Plate 46. fig. 9). This thin yellowish cap is so hard and brittle that it is frequently splintered by the pressure of the covering-glass, and is always lost when the tooth is rubbed down to reduce it in thickness, as it easily breaks off bodily.

This enamel cap disappears altogether in decalcified sections, in which, therefore, the bifid character of the tip of the tooth becomes quite inconspicuous.

The teeth are but feebly attached, by anchylosis of the outer side of their bases, to a parapet of bone (fig. 1), the enamel-tipped apex of the tooth alone projecting above the level of the epithelium. The inner side of the base of the tooth descends to a much lower level, and either tapers to a thin edge, or is actually attached to a slight elevation of the bone (fig. 2).

The epithelium closely embraces the tooth on all sides where it emerges from it, forming a plane surface; and there is neither groove nor fissure in which the successional teeth are developed, as had been generally supposed (figs. 1 & 3).

In the place of the supposed groove there is, immediately to the inner side of the tooth and its supporting parapet of bone, a region which, to facilitate description, I will

* "Bei Siredon und Triton geht die Entwickelung der Zähne frei in der Schleimhaut vor sich; beim Frosche dagegen . . . . . in einem Zahnsäkchen."

† This bifid termination of the tooth was noted, I believe for the first time, by LEYDIG.

term the "area of tooth-formation," inasmuch as it contains nothing but structures concerned in the development of teeth.

Its outer limit has already been mentioned; on the inner side, toward the median line of the palate, it has no osseous boundary, but it is nevertheless very sharply defined by connective tissue (*e*, figs. 1, 2, 3, & 5).

At the surface, where it is continuous with the epithelium of the mouth, it is narrow; but as it becomes deeper it widens, so that the whole area* is roughly triangular in form, as is seen in figs. 2 & 3.

Along its basal or deepest portion, nearly, though not quite, resting upon the bone, are ranged, in horizontal series, two, three, or even four tooth-sacs, the youngest lying nearest to the middle line. A connexion between the apices of the sacs and the epithelium of the surface may be traced with more or less distinctness in every section through an elongated narrow neck of cells†; to the inner side of the youngest tooth-sac may also generally be seen a cæcal process of epithelial cells (*f*, in figs. 2 & 5), and to the inner side of this again another and shorter epithelial process, which does not extend so deeply (*f* in figs. 2 & 5).

The individual tooth-sacs are oval, very slightly flattened at their bases, and sharply defined; when it is so viewed that its surface is in focus, this is seen to be made up of a tesselated epithelium of great regularity, and when it is subjected to pressure it breaks up into a mass of cells‡ and nothing else (fig. 7).

The arrangement of the cells in the tooth-sac appears to have escaped the notice of previous writers, though it is to some extent analogous with that met with in Mammalia: there is a dentine-papilla, the cells upon the surface of which are arranged in an "odontoblast" layer (figs. 4 & 8); and outside this papilla, which is very soon capped with dentine, comes a layer of columnar epithelial cells, similar to the enamel cells or internal epithelium of the enamel-organ of mammals. At the base of the dentine-papilla this layer of columnar cells becomes continuous with a second layer of shorter cells, which lie externally, and constitute the tesselated epithelium already mentioned as forming the surface of the sac (figs. 4, 5, 6). The "enamel-organ" is therefore, like that of the armadillo, made up wholly of the two layers of cells, without any intermediate tissue.

The continuity of the cells constituting the enamel-organ with the epithelial processes or necks before alluded to can generally be traced (figs. 1, 2, 3, 5, 6).

The base of the dentine-papilla is sharply defined, and no crescentic processes pass up from it around the outside of the enamel-organ, to take a share in the formation of

* The upper jaw has been selected for description because the tooth-sacs are less crowded together than in the lower jaw.

† This was mentioned by Dr. LIONEL BEALE, who, however, did not trace out its developmental origin; and it was observed also by Professor HUXLEY in the tooth-sac of the mackerel.

‡ Although there may be some theoretical difficulties in the way of accepting this, I am, after repeated examination, inclined to concur in the opinion very positively expressed by Dr. BEALE, that these sacs have no limiting membrane whatever.

a capsule, as happens in a mammalian tooth-sac; and although the fibres of the connective tissue are to some slight extent pushed on one side, so as to be in some measure concentrically ranged round the growing tooth-sac, yet they do not form any thing like a definite investment to it. Vessels are abundant in the immediate neighbourhood of the tooth-sacs; but they do not appear to enter them, save when the tooth is somewhat advanced.

Although I have never been fortunate enough to obtain a specimen in which the first tooth-sacs were in process of formation*, yet, owing to the very large number of successional teeth which are formed, it is possible to trace out all the stages of the process in an adult animal.

The processes of epithelium which are to be found on the inner side of the youngest tooth-sacs have already been mentioned; they are very well seen in figs. 2 & 5 (f & f_1): thus in fig. 5 we have three stages in the formation of a tooth-sac—namely, the earliest dipping down of epithelium, as seen at f_1, and an epithelial process which has reached down nearly to the base of the area of tooth-development, while to the right of this is a fully formed tooth-sac, which, however, still retains its connexion with the epithelial cells above it.

These epithelial processes, shooting down from the surface into the connective tissue below, which they push out of their way, are clearly homologous with the "enamel-germs" of mammalian teeth; and just as the enamel-germ of a human permanent tooth is given off from the neck of cells which connects the enamel-organ of the deciduous tooth-sac with the oral epithelium, so in these Batrachian teeth the enamel-germs of the successional teeth are given off from those of their predecessors† (see figs. 5 & 7).

When the end of the epithelial process has nearly reached to the base of the area of tooth-formation, its cells become more distinctly columnar in character, and its end enlarges, so that it has a spherical form when viewed on its surface; but seen in section it presents the appearance shown in fig. 6, in which the extremity of the enamel-germ has assumed the form of a bell-shaped cap, embracing the dentine-papilla inside it. At this early period the cells of the enamel-germ next to the dentine-papilla are elongated; and the dentine-papilla shows indications of the bicuspidate form of the crown in one of my sections (fig. 8), though this may perhaps be accidental, as I have not seen it constantly.

A peculiarity in the appearance of the tooth-sacs of the newt is that they are very

* Professor Huxley informs me that tooth-development in the newt commences at a very much earlier period than in the frog.

† This reopens the question, are the milk or the permanent teeth of diphyodonts homologous with the single set of monophyodonts?—a question which appeared to have been set at rest by Professor Flower's paper (Journal of Anatomy and Physiology, 1869). The arguments in that paper appeared to be conclusive in favour of the view that the milk-dentition was the thing superadded; but this is difficult to reconcile with the developmental relation existing between tooth-germs of the two.

sharply defined and mapped off from surrounding tissues from the very first. The dentine-papilla gives rise to no prolongations from its base; but the whole tooth-sac is at first nearly spherical (figs. 6, 7, & 8), and I have failed in any section to clearly see that the dentine-papilla has an origin distinct from the enamel-germ. Nevertheless the close resemblance borne by the completed tooth-sac of the newt, as well as the identical relations displayed by its enamel-germ, to that of the *Anguis fragilis* and green lizard, in which I have succeeded in tracing the whole process, as well as the *primâ facie* improbability of such a view, leads me to reject the views advanced by Dr. LIONEL BEALE and LEYDIG, that the whole tooth, including the dentine, is derived from an epithelial origin*.

Common Frog.—The general features of the process are closely similar to those observed in the newt, although there are many differences of detail.

The region designated as the area of tooth-development, which extended far into the palate in the newt, is very circumscribed in the frog, so that there is not room for more than one successional tooth-sac at one time (Plate 47. figs. 11, 12, 13).

And instead of the successional tooth-sac attaining to a considerable size without noteworthy encroachment on neighbouring structures, it obtains space and at the same time protection by the absorption of a portion of the bony parapet carrying the teeth or of the tooth itself (see figs. 12 & 13); thus it is not very unusual for the whole tooth-sac to pass bodily into what corresponds to the pulp-cavity of the tooth already in place (fig. 12).

This recession of the tooth under some shelter is in a measure a necessary consequence of the peculiar antagonism of the upper and lower jaws.

The lower jaw has a smooth rounded border and no vestige of a lip; when the mouth is closed it passes not only within the upper lip, but also within the teeth and their supporting parapet of bone (see diagrammatic section, fig. 10), and is received into a groove, which it closely fits, formed between the maxillary parapet and an inward jutting process which fits beneath the very peculiar tongue (figs. 10 & 11). Of the

* Dr. LIONEL BEALE says, "The tooth is not developed from a papilla, consisting of subbasement tissue, but it is formed in the very centre of a collection of cells; and it is clear that these cells have been formed in the central part of a preexisting cellular mass, so that the oldest cells, which seem but to perform the office of a protecting envelope, are outside, and, as new ones have been produced in the centre, these oldest cells have become somewhat flattened on the surface, thus giving the appearance of a boundary or imperfect capsule, which enables us to distinguish these masses from the collection of cells in which they are imbedded.

"I have seen a single cell, differing from its neighbours in its larger size, dividing to form three or four separate cells; and I believe this was the original cell from which all those which constitute the collection in which the tooth at length appears resulted."

In this account neither the intimate structure of the sac nor the share taken by the dipping inwards of the epithelium is mentioned; nor was LEYDIG more explicit in his descriptions.

What is meant by SANTI SIRENA in the statement that the tooth of the newt is developed free in the mucous membrane, I do not exactly know; but it is clear that he cannot have recognized the very definite structures which exist, or he would hardly have so expressed himself.

teeth only just the extreme tips project beyond the surface of the epithelium, so that their functional importance can be but small.

On its inner side the area is, as in the newt, bounded by a connective-tissue framework only (figs. 12, 13, & 14), which is in appearance very different from the tissue occupying the residual space within the area. The tooth-sacs themselves differ but little from those of the newt, though the columnar character of the cells composing the inner layer of the enamel-organ is less strongly marked*.

The connective tissue which is in the neighbourhood of a forming tooth-sac becomes to some extent arranged round it, though nothing amounting to a definite connective-tissue capsule is formed; indeed I have never been able to satisfy myself of the existence of a membranous investment to these sacs, though I would not go so far as to deny its existence.

The first step towards the formation of a sac is that inflection of the oral epithelium (*f* in figs. 12, 13, 14) which ultimately forms the enamel-organ; but the connexion between this latter at the apex of the sac with the oral epithelium is not long traceable, for the tooth-sac is so close beneath the surface, that it comes to be in contact with the epithelium along a considerable part of its circumference (figs. 11 & 13).

In close relation with the inner boundary of the tooth-sac is to be found the enamel-germ for the successional tooth-sac (*f*, fig. 13); but whether this arises directly from the epithelium, starting anew, as it were, for the formation of each tooth, or is derived from the cells going to form its predecessor, is very difficult to determine, as the migration of the growing sac speedily masks its origin and would destroy any such connexion. Hence the enamel-germs often stand alone, as in figs. 14 & 12; and appearances lead to the supposition that their origin is quite independent of previous tooth-germs.

After the tooth has attained to nearly its full size and is displacing its predecessor, the formative dentine-pulp undergoes change; the distinct character of the odontoblast layer is lost, and it becomes metamorphosed into a close-meshed connective-tissue reticulum, poor in vessels, a single vascular loop being usually all that it presents (fig. 11). The tooth becomes attached to the bone more securely than that of the newt, for it is mounted on a more complete pedestal (fig. 11), and not merely soldered on by its outer edge; the inner buttress of bone (*d* in fig. 11) is not, however, complete, but is perforated to admit vessels, and also often excavated by the successional tooth-sac.

In the frog, therefore, just as in the newt, there is no such thing as a dental groove, no such thing as free dental papilla, and no process of encapsulation such as GOODSIR conceived†.

* If any enamel at all is formed, it is only an exceedingly thin layer. Prof. OWEN described an investment of enamel on the convex surface only, and a layer of cement on the concave surface, a distinction in which I am unable to follow him. WALDEYER says that OWEN is altogether mistaken in supposing that the frog has any enamel at all, while Prof. HUXLEY speaks of the existence of an exceedingly thin layer of enamel.

† Professor OWEN (Odontography, p. 185) writes:—"In the frog the dental germ makes its appearance in

Anguis fragilis and *Lacerta viridis.*—The descriptions of these two forms may be most conveniently taken together, as no differences of importance have to be recorded between them. The area of tooth-development exists in them as a sharply defined region, bounded on its inner side by connective tissue, just as in the newt and the frog; but although it is not restricted by extraneous causes, such as the antagonism of the upper and lower jaws, it nevertheless is not widely extended as in the newt, but contains only one advanced tooth-sac at one time (Plate 47. figs. 16, 17, 18). The tooth-sac acquires a more definite connective-tissue investment than was the case in the frog (fig. 19 and the right-hand lower corner of fig. 22); but this investment, so far as it can be said to be such, seems to be mainly due to the displacement of a loose connective tissue in front of the growing tooth-germ, and it plays no active part in the formation of the tooth. The base of the dentine-papilla also is not so sharply cut off as in the newt and frog, but it shows an appearance of prolongation from its base upwards around the end of the enamel-organ (fig. 19).

The enamel-germ appears to be given off from that of the preceding tooth-sac (fig. 19); at least a process is very often discoverable at the side of this latter, although the connexion with the oral epithelium is not lost and appears to be tolerably direct (see figs. 18 & 16): I am inclined to think that the enamel-germs do not arise from the oral epithelium quite *de novo* for each tooth-sac, but that they may be justly described as successive branches of a common stem. An early stage of a tooth-sac is represented in fig. 20, in which the dentine-papilla is seen to be distinct in its origin from the enamel-organ, but to be a portion of the tissue into which this latter dips down, and to be quite continuous with the connective tissue which forms an adventitious investment to the whole sac and to the elongated neck of epithelial cells above it.

The cells which lie upon its surface become elongated to form an odontoblast layer or membrana eboris, and the whole dentine-papilla speedily becomes differentiated from the tissue around from which it took its origin.

The enamel-organ presents no special peculiarity; the inner layer of cells is distinctly columnar, and the outer more nearly spherical, the enamel-organ consisting exclusively of these two layers with no intermediate structure (figs. 19, 21).

When a cap of dentine, tipped slightly with enamel, has been formed, the odonto-

---

the form of a papilla developed from the bottom and toward the outer side of a small fissure in the mucous membrane or germ that fills up the shallow groove at the inner side of the alveolar parapet and its adherent teeth; the papilla is soon enveloped by a capsular process of the surrounding membrane; there is a small enamel pulp developed from the capsule opposite to the apex of the tooth; the deposition of the earthy salts in this mould is accompanied by ossification of the capsule, which afterwards proceeds *pari passu* with the calcification of the dental papilla or pulp; so that, with the exception of its base, the surface of the uncalcified part of the pulp alone remains normally unadherent to the capsule." That there is no papillary stage was pointed out by Prof. HUXLEY (*loc. cit.*), who, however, did not trace out all the details of the process, and makes no particular mention of the epithelial inflections; as to the latter part of Prof. OWEN's description, I have never observed any thing which could be called ossification of the capsule, if, indeed, there be such a structure as the capsule at all in the sense in which he employs it.

blast layer (*o* in fig. 22) is very clearly to be seen; and where it has been accidentally displaced to a slight extent, the dentinal fibrils discovered in the human tooth by my father may be seen like harp-strings stretching across to the dentine (fig. 22). Beneath the odontoblast layer comes an areolar tissue framework, much like that which occurs in mammalian tooth-pulps. Thus in the teeth of the lizards the tooth-pulp attains to a higher organization, and is less soon converted into a mere connective-tissue reticulum, than in the newt and frog; and although we have no actual basis of observation to rest upon, it is therefore highly probable that the durability of each individual tooth after it has become attached to the jaw is greater. As the tooth moves up into position the whole of the structures comprised in the tooth-sac, including the outer loose and ill-defined investment of connective tissue, go with it.

When its outer border reaches the level of the top of the alveolar parapet (as in figs. 16 & 21) it comes into contact with a tolerably well-defined band of connective tissue, which runs up from the apex of the bone towards the epithelium of the surface (*m* in fig. 21), and, when there is no tooth in place, bounds the area of tooth-formation on its outer side. This is continuous with the periosteum, and probably plays an active part in securing the tooth to the bone; it may be invariably recognized when a tooth is nearly in place, and was seen by Professor HUXLEY, who mentions that a membrane may be traced on to the tooth of the frog from the outer surface of the bone. The precise manner in which the succession and attachment of the teeth is effected is a matter of much interest, but is rather beyond the scope of the present communication.

The enamel-organ with its double layer of cells remains distinctly recognizable up to the time when the tooth comes into position on the bone; as it does not quite reach to the base of the dentine-papilla (see fig. 21), it does not intervene between the dentine and the apex of the bone and its periosteum; it is lost sight of afterwards*.

On the inner side the characteristic folding over of its cells, where the inner merges into the outer layer, may be seen after the tooth is in place, closely applied to the surface of the tooth (see fig. 18).

As this row of cells intervened between the dentine and the capsule, it is quite certain that the tooth cannot have received any investment from the ossification of the capsule.

Before any generalizations can advantageously be drawn from these or any other observations, the subject of the development of the teeth in Fishes† requires further elucidation; and some investigations which I have commenced in that direction are not as yet sufficiently extensive to serve as a basis for general statements. The tooth-sacs of the *Anguis fragilis* and *Lacerta viridis* are, however, instructive, inasmuch as they are deve-

* My preparations do not enable me to speak with absolute certainty as to the ultimate disposal of the enamel-organ; the point requires further investigation.

† The only reliable description of the tooth-sac of a fish with which I am acquainted, is given by Professor HUXLEY in the paper already several times quoted.

loped in the midst of mature structures, whereas the tooth-sac of Mammalia arises in the midst of embryonic tissue.

The substantial identity of the dentine-papilla and of such capsule as exists is well shown in fig. 20, where the structures going to form the capsule are continuous and blended with the forming dentine-papilla; while above this the perfectly distinct origin of the enamel-organ from an exceedingly elongated process of the oral epithelium is clearly seen.

A comparison of the tooth-sacs of the newt, frog, and lizard shows many points of close resemblance, the most noteworthy difference being in the extent to which a capsule is derived from the base of the dentine-papilla. In the newt the dentine-papilla ends abruptly, contributing absolutely nothing to the formation of a capsule external to the enamel-organ, so that the tooth-" sac" is devoid of a capsule (Plate 46. fig. 6); in the frog it does appear to take some very slight share in the formation of an imperfectly defined capsule (Plate 47. fig. 15); while in the lizard it is distinctly continuous with a sort of capsule (Plate 47. fig. 19), which is recognizable at all stages of the development of the tooth.

In this respect, therefore, as also in the structure of the tooth pulp, the lizard approximates more closely to the structure of the mammalian tooth-sac than do the others.

The much vexed general question as to the existence of a "membrana præformativa" can be more profitably discussed when our knowledge of the tooth-sacs of fishes is more definite; but nevertheless a few words about it may not be out of place here.

A "membrana præformativa," in the sense in which the older writers used the term, viz. as a membrane covering the "dental papilla" in common with the rest of the surface of the mucous membrane, clearly cannot be said to exist, seeing that the changes resulting in the formation of a dentine-papilla take place far below the surface, in the solid substance, so to speak, of the connective tissue. If there is at any time a membrane proper to the dental papilla, it is a special subsequent formation, having nothing to do with the basement membrane, and is in its origin quite a different thing from the membrana præformativa as originally conceived.

It is quite possible, however, that the offshoot from the oral epithelium may carry down in front of it during its descent into the submucous tissue a pouch of basement membrane, which would in this case intervene between the enamel-cells and the dentine-papilla, though it would belong to the former rather than to the latter. Although there would seem to be an *à priori* probability in this supposition, the appearances presented by the epithelial processes in the frog (Plate 47. fig. 14) do not favour the supposition that they are bounded by a membrane; they are distorted and destroyed by very slight pressure or very slight pencilling; and in the case of the newt, after a tooth-sac and its surroundings are broken up by pressure, I can discover nothing whatever but cells.

And, again, the manner in which the connective tissue outside the area of tooth-

formation in the newt sends up its branching fibres through the epithelium, reaching almost to its surface (Plate 46. figs. 2, 3, 5), renders it difficult to suppose that a basement membrane intervenes between it and the epithelium. But there is no such difficulty in the case of the frog, in which animal the boundary-line of the epithelium is less irregular; and it must be admitted that there is an *à priori* probability in the enamel-germ being enclosed within a basement membrane, if this exists between the oral epithelium and the subjacent tissues; so that I am unable to speak more positively than to say that I have uniformly failed in demonstrating the existence of such a membrane.

Explanation of the Plates.

PLATE 46.

a. Tooth-bearing process of maxillary bone.
b. Oral epithelium.
c. Neck of epithelial cells connecting the tooth-sac with the oral epithelium.
d. Young tooth-sac.
e. Dense connective tissue, forming the internal limit to the area of tooth-formation.
f, f_1. Processes of epithelium (=enamel-germs of Kölliker) which will ultimately participate in forming tooth-sacs.
h. Formative pulp of the dentine.
k. Cap of dentine.
l. Columnar epithelium of the enamel-organ (enamel cells).
m. Connective-tissue band on the outer side of the area of tooth-formation.
o. Odontoblast layer of dentinal pulp.
t. Completed tooth.

Figs. 1 to 9. From the upper jaw of *Triton cristatus.*

Fig. 1. From newt half-grown, $\times$ 50.
Fig. 2. From newt half-grown (the lip is omitted from this figure), $\times$ 50.
Fig. 3. From adult specimen. Teeth in four stages of development are seen within the area, $\times$ 50.
Fig. 4. Young tooth-sac in which the cap of dentine is just formed, $\times$ 120.
Fig. 5. Young tooth, showing its relations with the oral epithelium and with the successional enamel-germ, $\times$ 200.
Fig. 6. Termination of epithelial process, commencing to form the enamel-organ of a very young tooth-sac, $\times$ 220.
Fig. 7. Young tooth-sac, viewed on its surface, which is seen to be a tesselated epithelium, $\times$ 220.
Fig. 8. Very young tooth-sac, showing odontoblast layer.

Fig. 9. Apex of tooth, with its enamel cap undisturbed; the odontoblast layer is also seen, × 400.

Fig. 11. Lip and margin of upper jaw of full-grown frog, with tooth in place and to its normal extent, × 50.

Fig. 20. Young tooth-germ of *Lacerta viridis*, × 400, from the same section as fig. 18.

PLATE 47.

Lettering the same as Plate 46.

Figs. 10 to 15. Common Frog.

Figs. 16 to 22. *Anguis fragilis* and *Lacerta viridis*.

Fig. 10. Diagrammatic section of upper and lower jaws of a common frog, × 5.

Fig. 11. See Plate 46.

Fig. 12. Successional tooth-sac beneath the tooth in place; enamel-germ very distinct, × 120.

Fig. 13. Successional tooth-sac partly buried in the tooth-bearing parapet of bone, × 80.

Fig. 14. Relations of enamel-germ to the area of tooth-formation and to the maxillary bone, × 220.

Fig. 15. Young tooth-sac prior to the formation of dentine, × 250.

Fig. 16. Upper jaw of *Anguis fragilis*, showing a tooth ascending into position, a successional tooth-sac, and the connective tissue to the right of the area of tooth-formation, × 40.

Fig. 17. Lower jaw of the same, × 40.

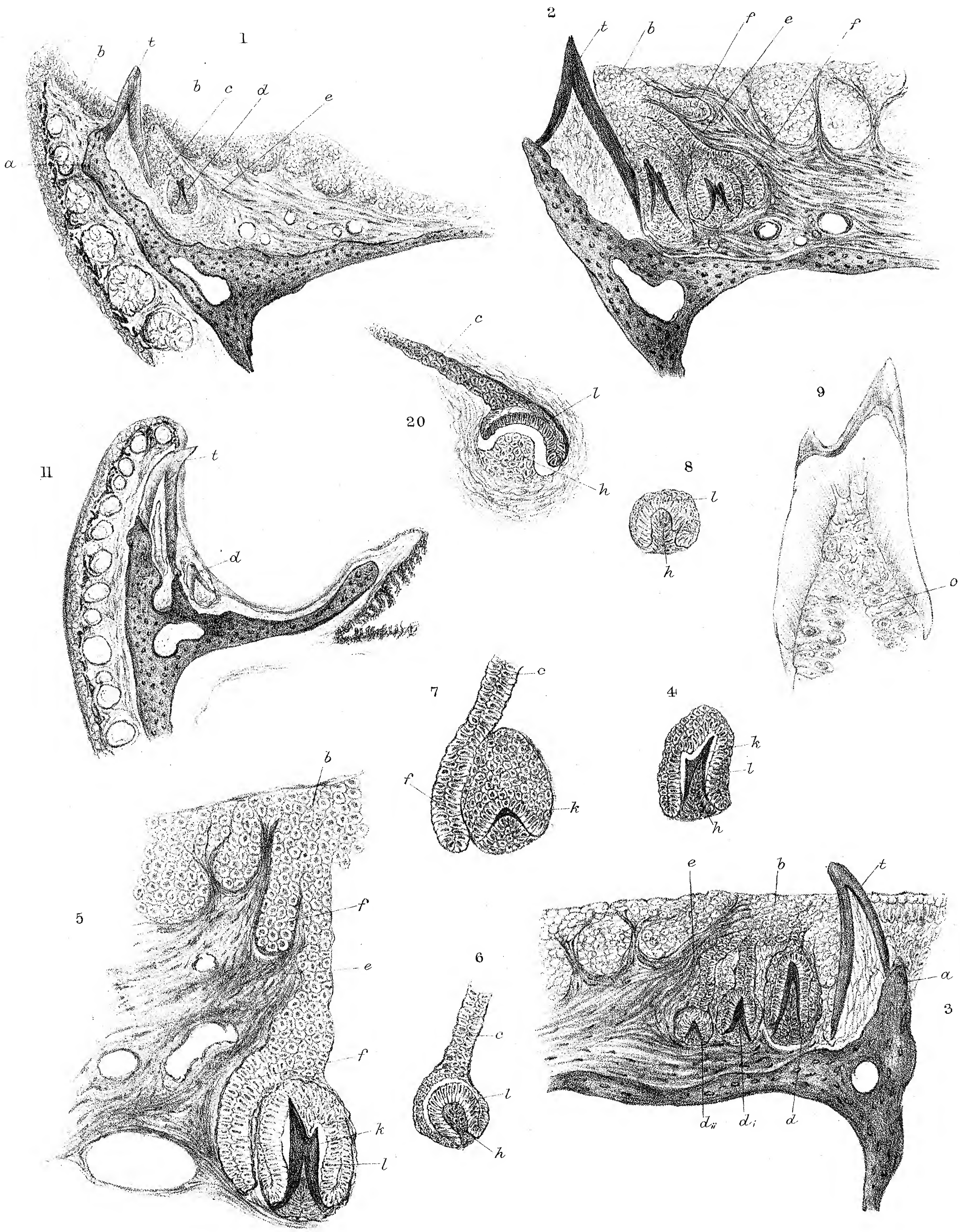
Fig. 18. Upper jaw of *Lacerta viridis*; to the right of the perfected tooth is a very early tooth-sac, × 150.

Fig. 19. Young tooth-germ of *Anguis fragilis*, × 500.

Fig. 20. See Plate 46.

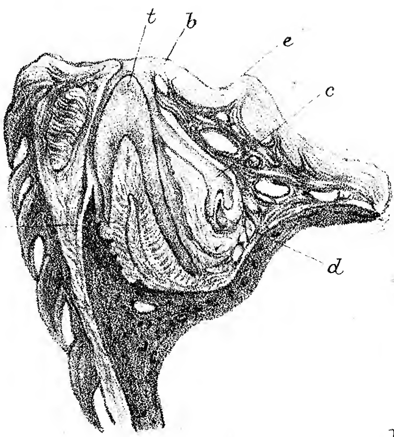
Fig. 21. Relation of tooth-sac to oral epithelium. The band of connective tissue (*m*) at the top of the bone, which takes a share in cementing on the teeth, is well seen (*Anguis fragilis*). × 150.

Fig. 22. Apex of a forming tooth; the odontoblast layer of the pulp, with the dentinal fibrils stretching across to the dentine, is well seen, × 300.

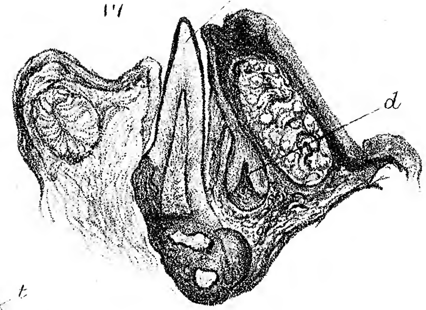


E. M. Williams F.L.S. F.Z.S. lith.
W. West & C.º imp.

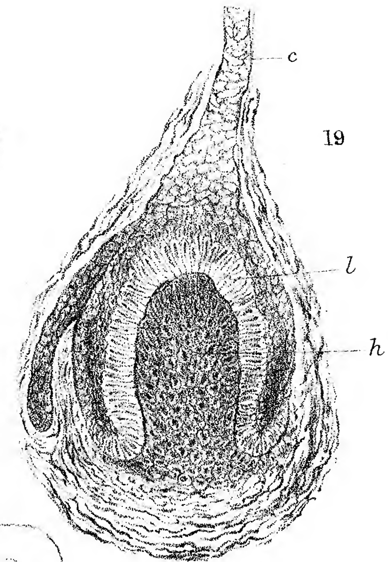
16



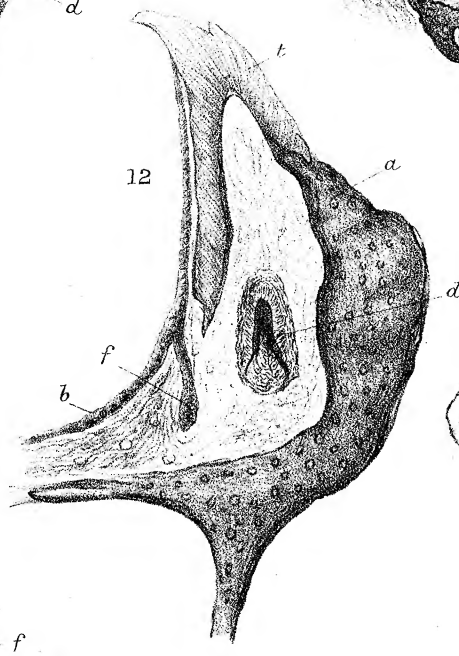
17



19

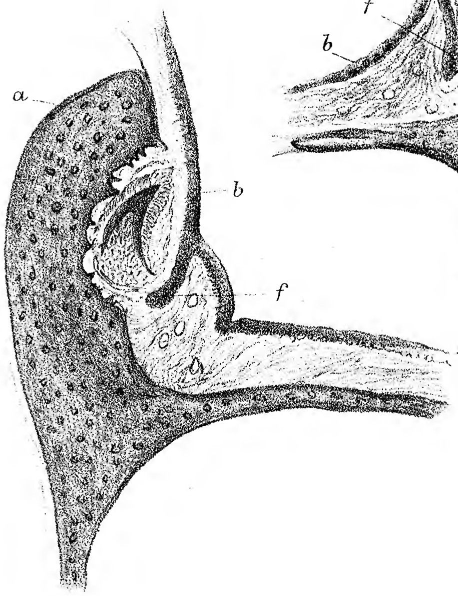


12

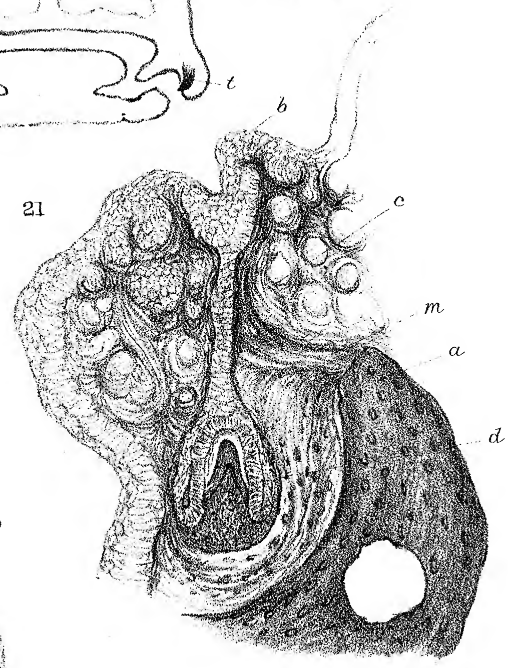


10

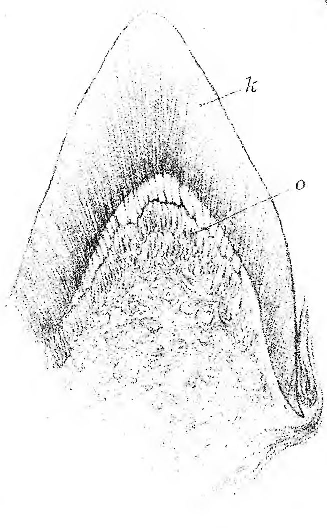
13



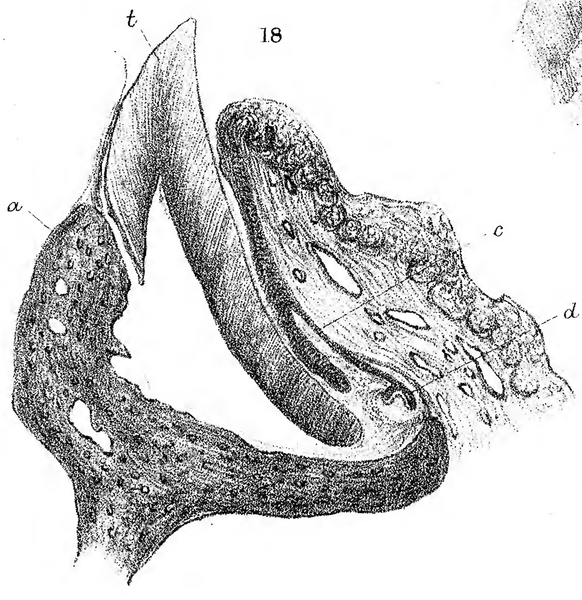
21



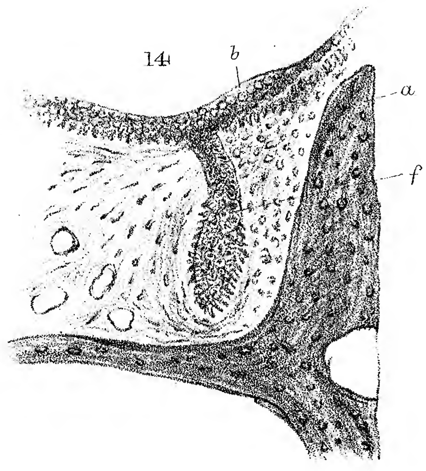
22

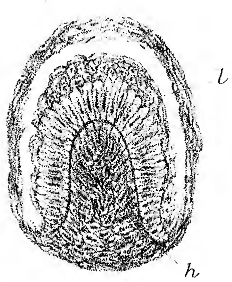


18



14





15

E. M. Williams F. L. S. F. Z. S. lith.